

**Abstract**—In the original von Bertalanffy growth equation, the rate of change in body mass of an individual is assumed to result from two opposing biological processes: anabolism and catabolism. Because this differential equation cannot be solved analytically, some of its analytically solvable special cases are commonly used, despite their restrictive assumptions. In this study, I used a generalization of the original von Bertalanffy growth equation and some of its commonly used special cases to estimate parameters from a set of tagging data on times at liberty, lengths at release, and lengths at recapture of a centropomid perch (*Lates calcarifer*) and provide a method for determining the anabolic and catabolic rates of animals in their natural environment. Fitting the original von Bertalanffy growth equation to the tagging data suggests that a 1% increase in body mass of the fish corresponds to a 0.8721% increase in anabolic rate and a 1.0357% increase in catabolic rate. Alternatively, *L. calcarifer* may be interpreted as exhibiting a strong seasonality in growth: it grows fastest in length at the start of autumn, grows less until a full stop in the middle of winter, shrinks until the middle of spring, and then resumes a positive growth for another cycle. Consequently, it is unnecessary to use the analytically solvable special cases of the original von Bertalanffy growth equation in data analysis, unless their assumptions are validated. I also explain why Pauly's index of growth performance is adequate and propose an index of catabolic performance.

## Use of the original von Bertalanffy growth model to describe the growth of barramundi, *Lates calcarifer* (Bloch)

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Information on the growth of animals is important for studying their population dynamics, physiology, and biochemistry (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Reiss, 1989; Xiao, 1998). Many empirical models have been developed to describe the growth of animals macroscopically, including the Gompertz (1825) and logistic growth models (Verhulst, 1838). By contrast, von Bertalanffy (1938) proposed a somewhat mechanistic growth model for body mass  $W(a) \geq 0$  of an individual of age  $a$ , of the form

$$dW(a)/da = AW(a)^B - CW(a)^D,$$

where  $A$ ,  $B$ ,  $C$  and  $D$  = positive biological constants;

$AW(a)^B$  = the rate of anabolism (building up of body mass) at age  $a$ ; and

$CW(a)^D$  = the rate of catabolism (breaking down of body mass) at age  $a$ .

Thus, in this model, the rate of change in body mass of an individual  $dW(a)/da$  at age  $a$  is assumed to result from two opposing biological processes (anabolism and catabolism). Although the underlying mechanisms may be too complicated for  $dW(a)/da$  to be approximated or even interpreted as such, this differential equation has opened up a line of thought for integrating the macroscopic growth of animals with certain physiological and biochemical processes (Pauly, 1981). Also, it is fairly general, includes almost all previous deterministic growth models as its special cases,

and forms a basis for identifying the "right" growth models from amongst all its special cases. Consequently, some work has been done to estimate parameters  $A$ ,  $B$ ,  $C$ , and  $D$  to determine the anabolic and catabolic rates of fish (Ursin, 1967; Pauly, 1981).

However, because the differential equation cannot be solved analytically, its analytically solvable special cases are so commonly used that one simple special case has become known in the fisheries literature as *the* von Bertalanffy growth equation (Xiao, 1996). Nonetheless, assumptions for its various analytically solvable special cases can be very restrictive. Indeed, although assumed to take a value of  $2/3$  in that simple special case (Pauly, 1981), constant  $B$  can take any value from  $2/5$  to  $5/7$ , because  $B$  is often assumed to satisfy  $\beta(B-1)+1=0$  and because  $B$  in Equation 2 below is known to take any value from  $2^{1/2}$  to  $3^{1/2}$ . It is also possible that catabolic rate is not proportional to body mass (i.e.  $D \neq 1$ ). In any case, it is best not to make any assumptions about the values of  $A$ ,  $B$ ,  $C$ , and  $D$ .

Like most growth models, the von Bertalanffy (1938) growth equation is age-dependent. Although it can be modified to consider, implicitly, the seasonal growth of animals and the effects of tagging, a general framework was not available for explicitly incorporating time and time-dependent factors (i.e. ambient temperature and food availability) in age-dependent growth models. This prompted Xiao (1999) to derive general age- and time-dependent growth models for animals and to give a comprehensive list of their commonly used special cases. Such models explicitly incorporate age, time, and their de-

pendent factors and are useful for modeling growth at age and time (e.g. from length-at-age data), incremental growth at age and time increment (e.g. data on length increment at age and time increment from tagging studies), the effects of tagging, and, if coupled with a proper age- and time-dependent population dynamics model, the effects on the growth of animals of many population characteristics, such as population size.

Because of experimental constraints, such as difficulties in taking continuous measurements (if measured at all), anabolic and catabolic rates of animals are necessarily measured either by restraining them in the laboratory or in the field. Such restraints can cause stress to animals and hence result in biased measurements. Experimental methods should be developed to estimate the anabolic and catabolic rates of animals in as natural an environment as possible.

In this study, I use an age- and time-dependent von Bertalanffy (1938) growth equation and some of its commonly used special cases for estimating the parameters from a set of tagging data on times at liberty, lengths at release, and lengths at recapture of a centropomid perch, barramundi (*Lates calcarifer*) and provide a method for determining the anabolic and catabolic rates of animals in their natural environment. I also explain why Pauly's (1981) index of growth performance is adequate and propose an index of catabolic performance.

**Model**

Let  $0 \leq W(a,t) < \infty$ ,  $-\infty < a_0 \leq a < \infty$ ,  $-\infty < t_0 \leq t < \infty$ , denote the body mass of an individual of age  $a$  at time  $t$ , with an arbitrary reference age  $a_0$  and an arbitrary reference time  $t_0$ . The von Bertalanffy (1938) growth equation can be generalized as

$$\frac{dW(a,t)}{dt} = A(a,t)W(a,t)^B - C(a,t)W(a,t)^D, \tag{1}$$

where  $A(a,t) \geq 0$  and  $C(a,t) \geq 0$  = functions of age  $a$  and time  $t$ ; and  
 $B$  and  $D$  = positive biological constants.

For a particular functional form of  $A(a,t)$  and  $C(a,t)$ , Equation 1 can be used for estimating its parameters from data on body masses of animals of different ages at different times, or on two distinct body masses of the same individual at different times. If collected at all, such data are collected mostly for terrestrial and occasionally for aquatic animals. What is most commonly gathered for both terrestrial and aquatic animals is, however, one or more linear dimensions of an individual's body, such as its total length at age, or two distinct measurements at different times. Measurements of linear dimensions of an animal contain useful information on its body mass. Indeed, it is well known that body mass  $W(a,t)$  is scaled allometrically to body length  $L(a,t)$ , i.e.

$$W(a,t) = \alpha L(a,t)^\beta, \tag{2}$$

where  $\alpha$  and  $\beta$  = (constant) allometric parameters (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Reiss, 1989).

Substitution of Equation 2 into Equation 1 yields

$$\begin{aligned} \frac{dL(a,t)}{dt} &= \frac{1}{\beta} \alpha^{B-1} A(a,t) L(a,t)^{\beta(B-1)+1} \\ &\quad - \frac{1}{\beta} \alpha^{D-1} C(a,t) L(a,t)^{\beta(D-1)+1}. \end{aligned} \tag{3}$$

Thus, if  $\alpha$  and  $\beta$  are known, as is usually assumed, parameters  $B$  and  $D$ , and those in  $A(a,t)$  and  $C(a,t)$  can be estimated from data on length-at-age data, or on two distinct lengths of the same individual at different times.

Although too general to be solved even numerically, Equations 1 and 3 are useful in formulating ideas. Now, I consider a special case of Equations 1 and 3 for seasonally varying  $A(a,t)$  and  $C(a,t)$ , such that

$$\begin{aligned} A(a,t) &= \frac{\gamma}{K} \left[ K + b \cos \left( \frac{2\pi}{T} (t - t_\phi) \right) \right] \text{ and} \\ C(a,t) &= K + b \cos \left( \frac{2\pi}{T} (t - t_\phi) \right), \end{aligned}$$

where  $\gamma$ ,  $\gamma b/K$ ,  $T$ , and  $t_\phi$  are, respectively, the mean, amplitude, period, and time shift for the anabolic process;  $K$ ,  $b$ ,  $T$ , and  $t_\phi$  are, respectively, the mean, amplitude, period, and time shift for the catabolic process. For this special case, Equations 1 and 3 then become, respectively

$$\begin{aligned} \frac{dW(a,t)}{dt} &= \left[ K + b \cos \left( \frac{2\pi}{T} (t - t_\phi) \right) \right] \\ &\quad \times \left[ \frac{\gamma}{K} W(a,t)^B - W(a,t)^D \right] \end{aligned} \tag{4}$$

and

$$\begin{aligned} \frac{dL(a,t)}{dt} &= \frac{1}{\beta} \left[ K + b \cos \left( \frac{2\pi}{T} (t - t_\phi) \right) \right] \\ &\quad \times \left[ \frac{\gamma}{K} \alpha^{B-1} L(a,t)^{\beta(B-1)+1} - \alpha^{D-1} L(a,t)^{\beta(D-1)+1} \right]. \end{aligned} \tag{5}$$

Equations 4 and 5 can be solved numerically but not analytically. For comparison and illustration, I now consider five special cases (four of which are reparameterizations of commonly used growth equations) of Equation 5:

If  $b=0$ , or if  $A(a,t)$  and  $C(a,t)$  are constants, Equation 5 becomes

$$\frac{dL(a,t)}{dt} = \frac{1}{\beta} \left( \gamma \alpha^{B-1} L(a,t)^{\beta(B-1)+1} - K \alpha^{D-1} L(a,t)^{\beta(D-1)+1} \right). \tag{6}$$

If  $\beta(B-1)+1=0$  (i.e.  $B-1=-1/\beta$ ) and  $\beta(D-1)+1=1$  (i.e.  $D=1$ ), Equation 5 becomes

$$\frac{dL(a,t)}{dt} = \frac{1}{\beta} \left[ K + b \cos\left(\frac{2\pi}{T}(t-t_0)\right) \right] \left( \frac{\gamma}{K} \alpha^{-1/\beta} - L(a,t) \right), \quad (7)$$

the solution of which as an initial value problem, with  $L(a,t)|_{t=t_0} = L(t_0 + a - t, t_0)$  for  $a - a_0 \geq t - t_0$  or with  $L(a,t)|_{a=a_0} = L(a_0, a_0 + t - a)$  for  $a - a_0 < t - t_0$ , yields

$$L(a,t) = \begin{cases} \frac{\gamma}{K} \alpha^{-1/\beta} - \left( \frac{\gamma}{K} \alpha^{-1/\beta} - L(a_0, t - a + a_0) \right) \\ \times \exp\left( -\frac{K}{\beta}(a - a_0) - \frac{bT}{\beta\pi} \sin\left(\frac{\pi}{T}(a - a_0)\right) \right) & a - a_0 < t - t_0 \\ \times \cos\left(\frac{2\pi}{T}\left(t - t_0 - \frac{1}{2}(a - a_0)\right)\right) \\ \frac{\gamma}{K} \alpha^{-1/\beta} - \left( \frac{\gamma}{K} \alpha^{-1/\beta} - L(t_0 + a - t, t_0) \right) \exp\left( -\frac{K}{\beta}(t - t_0) \right) & a - a_0 \geq t - t_0 \\ - \frac{bT}{\beta\pi} \sin\left(\frac{\pi}{T}(t - t_0)\right) \cos\left(\frac{2\pi}{T}\left(t - t_0 - \frac{1}{2}(t - t_0)\right)\right) \end{cases} \quad (8)$$

Similar age-dependent models have been given, *inter alia*, by Appeldoorn (1987), Pauly et al. (1992), Fontoura and Agostinho (1996), and Xiao (1999). Also, notice that  $bT$  (in Appeldoorn (1987) and Pauly et al. (1992),  $b=C$  and  $T=1$ ) is a dimensionless quantity and is useful for inter-specific comparison of the strength of seasonal growth oscillations (Pauly, 1984, 1985, 1990).

If  $\beta(B-1)+1=0$  (i.e.,  $B=1$ ),  $\beta(D-1)+1=1$  (i.e.,  $D=1$ ), and  $b=0$ , Equation 5 becomes

$$L(a,t) = \begin{cases} \frac{\gamma}{K} \alpha^{-1/\beta} - \left( \frac{\gamma}{K} \alpha^{-1/\beta} - L(a_0, t - a + a_0) \right) \\ \times \exp\left( -\frac{K}{\beta}(a - a_0) \right) & a - a_0 < t - t_0 \\ \frac{\gamma}{K} \alpha^{-1/\beta} - \left( \frac{\gamma}{K} \alpha^{-1/\beta} - L(t_0 + a - t, t_0) \right) \\ \times \exp\left( -\frac{K}{\beta}(t - t_0) \right), & a - a_0 \geq t - t_0 \end{cases} \quad (9)$$

a reparameterization of what is commonly called in the fisheries literature the von Bertalanffy (1938) growth equation.

If  $\beta(B-1)+1=0$  (i.e.,  $B=1$ ) and  $\beta(D-1)+1=2$  (i.e.  $D=1+1/\beta$ ), Equation 5 becomes

$$\frac{dL(a,t)}{dt} = \frac{\gamma}{\beta K} \left[ K + b \cos\left(\frac{2\pi}{T}(t-t_0)\right) \right] \times L(a,t) \left( 1 - \frac{L(a,t)}{\frac{\gamma}{K} \alpha^{-1/\beta}} \right), \quad (10)$$

the solution of which as an initial value problem, with  $L(a,t)|_{t=t_0} = L(t_0 + a - t, t_0)$  for  $a - a_0 \geq t - t_0$  or with  $L(a,t)|_{a=a_0} = L(a_0, a_0 + t - a)$  for  $a - a_0 < t - t_0$ , yields

$$L(a,t) = \begin{cases} \left[ \frac{1}{\frac{\gamma}{K} \alpha^{-1/\beta} - \left( \frac{1}{\frac{\gamma}{K} \alpha^{-1/\beta} - L(a_0, t - a + a_0)} \right)} \right]^{-1} \\ \times \exp\left( \frac{\gamma}{\beta}(a - a_0) - \frac{\gamma b T}{\beta K \pi} \sin\left(\frac{\pi}{T}(a - a_0)\right) \right) & a - a_0 < t - t_0 \\ \times \cos\left(\frac{2\pi}{T}\left(t - t_0 - \frac{1}{2}(a - a_0)\right)\right) \\ \left[ \frac{1}{\frac{\gamma}{K} \alpha^{-1/\beta} - \left( \frac{1}{\frac{\gamma}{K} \alpha^{-1/\beta} - L(t_0 + a - t, t_0)} \right)} \right]^{-1} & a - a_0 \geq t - t_0 \\ \times \exp\left( -\frac{\gamma}{\beta}(t - t_0) - \frac{\gamma b T}{\beta K \pi} \sin\left(\frac{\pi}{T}(t - t_0)\right) \right) \\ \times \cos\left(\frac{2\pi}{T}\left(t - t_0 - \frac{1}{2}(t - t_0)\right)\right) \end{cases} \quad (11)$$

a reparameterization of the seasonal logistic growth equation (Xiao, 1999).

If  $\beta(B-1)+1=1$  (i.e.,  $B=1$ ),  $\beta(D-1)+1=2$  (i.e.,  $D=1+1/\beta$ ), and  $b=0$ , Equation 5 becomes

$$L(a,t) = \begin{cases} \left[ \frac{1}{\frac{\gamma}{K} \alpha^{-1/\beta} - \left( \frac{1}{\frac{\gamma}{K} \alpha^{-1/\beta} - L(a_0, t - a + a_0)} \right)} \right]^{-1} \\ \times \exp\left( -\frac{\gamma}{\beta}(a - a_0) \right) & a - a_0 < t - t_0 \\ \left[ \frac{1}{\frac{\gamma}{K} \alpha^{-1/\beta} - \left( \frac{1}{\frac{\gamma}{K} \alpha^{-1/\beta} - L(t_0 + a - t, t_0)} \right)} \right]^{-1} \\ \times \exp\left( -\frac{\gamma}{\beta}(t - t_0) \right) & a - a_0 \geq t - t_0 \end{cases} \quad (12)$$

a reparameterization of the logistic growth equation (Xiao, 1999).

### Data and analysis

Equations 8, 9, 11, and 12 are segmented functions (Xiao, 1999); they provide flexibility in analysis of growth data. Thus, by appropriately choosing the value of time  $t$  (which is a relative quantity), one can use either segment ( $a - a_0 < t - t_0$  or  $a - a_0 \geq t - t_0$ ) for an individual animal or for a group of individuals, or use both segments ( $a - a_0 < t - t_0$  and

$a - a_0 \geq t - t_0$ ) for a group of individuals. It is, however, more convenient to use only one segment in a single analysis. Indeed, although growth parameters can be estimated by use of either segment of any of Equations 8, 9, 11, and 12, it is easier to use the segment for  $a - a_0 < t - t_0$ , by letting time  $t$  start before the animals whose growth is to be modeled are born, unless time is allowed to take negative values. Use of the other segment, i.e. that for  $a - a_0 \geq t - t_0$ , gives identical results, but it requires first calculating  $L(t_0 + a - t, t_0)$ .

The amount of data required to estimate parameters in a growth model is a function of the generality of that model: the more general a model is, the more data it usually requires. Age- and time-dependent growth models generally require knowledge of two ages  $a_0$  and  $a$ , time  $t$ , and two sizes  $L(a_0, t - a + a_0)$  and  $L(a, t)$  if  $a - a_0 < t - t_0$ ; or knowledge of two times  $t_0$  and  $t$ , age  $a$ , and two sizes  $L(t_0 + a - t, t_0)$  and  $L(a, t)$  if  $a - a_0 \geq t - t_0$ . However, use of Equations 4, 5, 8, and 11 only requires knowledge of the difference between two ages  $a - a_0$ , time  $t$ , and two sizes  $L(a_0, t - a + a_0)$  and  $L(a, t)$ ; or of the difference between two times  $t - t_0$ , time  $t$ , and two sizes  $L(t_0 + a - t, t_0)$  and  $L(a, t)$ . By contrast, use of Equations 9 and 12 only requires knowledge of the difference between two ages,  $a - a_0$ , and two sizes,  $L(a_0, t - a + a_0)$  and  $L(a, t)$ , or of the difference between two times  $t - t_0$ , and two sizes  $L(t_0 + a - t, t_0)$  and  $L(a, t)$ .

Interestingly, a reparameterization of Equation 9 has been widely used to model tagging data (Xiao, 1999), where  $a_0$  or  $t_0$  is interpreted as time at release,  $a$  or  $t$  as time at recapture,  $a - a_0$  or  $t - t_0$  as time at liberty,  $L(a_0, t - a + a_0)$  or  $L(t_0 + a - t, t_0)$  as size at release, and  $L(a, t)$  as size at recapture. It has also been used extensively to model size-at-age data (obtained, say, by aging animals by reading marks in scales and otoliths) (e.g. Moulton et al., 1992), where  $a_0$  or  $t_0$  is interpreted as age at birth,  $a$  or  $t$  as age,  $L(a_0, t - a + a_0)$  or  $L(t_0 + a - t, t_0)$  as size at birth, and  $L(a, t)$  as size at age. However, it is rare to know two ages and the corresponding sizes of an animal; what are commonly measured are one age and its corresponding size. Consequently, it is common practice to fit Equation 9 to such size-at-age data to estimate age at birth  $a_0$  or  $t_0$ , as well as the growth parameters, thereby implicitly assuming, for all animals concerned, that the size at birth  $L(a_0, t - a + a_0)$  or  $L(t_0 + a - t, t_0)$  is zero and that the age at birth  $a_0$  or  $t_0$  is the same. Exactly the same argument applies to Equation 12.

The barramundi *L. calcarifer* is a protandrous fish found in estuaries and other coastal areas of the Indo-West Pacific (Griffin, 1987). Between August 1977 and June 1980, 4933 barramundi with a body total length range of about 10–100 cm were captured by a combination of lure fishing, tidal trap, seine and gill net. Fish were measured to the nearest cm, tagged with Floy FT-2 dart tags for fish >35 cm and FD-67 anchor tags for fish <35 cm, and released in rivers flowing into the Van Diemen Gulf and the Gulf of Carpentaria of northern Australia (Davis and Reid, 1982). Of those tagged, 312 of a total length of 23–92 cm with a mean of  $60 \pm 13$  (mean  $\pm$ SE) cm were recaptured, but only 308 were used in the analysis below due to incomplete recapture information. The time at liberty ranged from zero to 932 d, with a mean of  $219 \pm 211$  d, and the

length increment from -21 to 35 cm, with a mean of  $6 \pm 8$  cm. Negative increments in length are often observed in a tagging experiment, because tagged animals can shrink in size immediately after tagging, or because of recording errors at both release and recapture. The estimates of allometric parameters for barramundi, used in the present paper, were those obtained by Reynolds (1978):  $\hat{\alpha} = 1.06 \times 10^{-5} \text{ kg} \times \text{cm}^{-\hat{\beta}}$  and  $\hat{\beta} = 3.02$ .

Let  $a_0$  or  $t_0$  denote time at release,  $a$  or  $t$  time at recapture,  $a - a_0$  or  $t - t_0$  time at liberty,  $L(a_0, t - a + a_0)$  or  $L(t_0 + a - t, t_0)$  the length of a fish at release, and  $L(a, t)$  its length at recapture. Equation 6 and the segments of Equations 8, 9, 11, and 12 for  $a - a_0 < t - t_0$ , were fitted to the tagging data, by using the nonlinear least squares method, under the assumptions that  $T = 365.25$  d, time started (i.e. time  $t = 0$ ) on 1 January 1960 (see Xiao [1999] for its significance), and errors in  $L(a, t)$  follow independent normal distributions, with a mean of  $\hat{L}(a, t)$  and a constant variance of  $\sigma^2$  (Table 1). In these calculations, Equation 6 was numerically solved as an initial value problem with  $L(a, t)|_{t=t_0} = L(t_0 + a - t, t_0)$  for  $a - a_0 \geq t - t_0$  using the fourth order Runge-Kutta method (Beyer, 1978). A likelihood ratio test suggests that Equation 8 is significantly different from Equation 9 ( $F_{2,304} = 48.6892, P < 0.0001$ ); and Equation 11 is significantly different from Equation 12 ( $F_{2,304} = 45.3460, P < 0.0001$ ). Thus, Equations 8 and 11, and their associated estimates of parameters seem adequate for describing the tagging data. Selection among Equations 6, 8, and 11 is difficult because little is known of the underlying mechanisms of the growth process.

## Discussion

Fitting of the original von Bertalanffy growth model (Eq. 6) to the tagging data for barramundi suggests that its anabolic rate changes proportionally with the  $\hat{B} = 0.8721$  power of its body mass and that its catabolic rate changes proportionally ( $\hat{D} = 1.03567 \approx 1$ ) with its body mass (i.e. at a 1:1 ratio). Such an estimate of  $B$  is 9.0125% higher than that ( $\hat{B} \approx 4/5$ ) obtained for many fish under laboratory conditions (Pauly, 1981). More data are needed to examine the generality of this finding. By contrast, little information is available on the value of  $D$ . Nonetheless, it is interesting that the catabolic rate of barramundi increases proportionally with its body mass; a 1% increase in body mass corresponds to about a 1% increase in catabolic rate. Consequently, it is unnecessary to use the analytically solvable special cases of the original von Bertalanffy growth equation in data analysis, unless their assumptions are validated.

Alternatively, like many tropical and subtropical species of fish (Appeldoorn, 1987; Pauly et al., 1992), barramundi may be interpreted as exhibiting a strong seasonal growth. For both models (Eqs. 8 and 11), its growth rate reaches its maximum on 3 or 4 March (i.e. at the start of autumn), slows down to zero on 17 July (i.e. in the middle of winter), reaches its minimum on 2 or 3 September (i.e. at the start of spring), returns to zero on 19 or 20 October (i.e. in the middle of spring), and comes back to its maxi-

mum rate on 3 or 4 March (i.e. at the start of autumn) (Fig. 1). Thus, its length grows fastest on 3 or 4 March (i.e. at the start of autumn), grows less until a full stop on 17 July (i.e. in the middle of winter), shrinks until 19 or 20 October (i.e. in the middle of spring), and resumes a positive growth for another cycle. Thus, barramundi does not grow in length for three months in a year, from 17 July (i.e. in the middle of winter) to 19 or 20 October (i.e. in the middle of spring). However, Equations 8 and 11 have different assumptions and predict different amplitudes of seasonally varying growth rate. Such a strong seasonality in growth rate might be related to seasonal changes in the availability of food and in water temperature.

Similarly, tagging may adversely affect the growth of barramundi perch and bias estimates of parameters in a growth model, where its effects are not taken into proper account. In fact, Xiao (1994) has already interpreted the same set of data in terms of the effects of tagging. However, it is impossible to identify the right model from all possible models, because of the inductive nature of modeling and because of our poor understanding of the underlying mechanisms of growth and how tagging affects growth. In a preliminary analysis, I have constructed a model, and have attempted (but failed) to estimate, simultaneously, both the effects of tagging and seasonally varying growth rates. Such a failure is not surprising because the amount of information in a set of tagging data is limited. Further progress can be made only by better understanding the underlying mechanisms of growth.

This work also puts some of Pauly's (1981) work into perspective. For example,  $\alpha^{-1/\beta}\gamma/K$  and  $K/\beta$  in Equation 9 can be interpreted respectively as the average maximum size and growth rate of a species. As Pauly (1981) proposed, the product  $(\alpha^{-1/\beta}\gamma/K)(K/\beta) = \alpha^{-1/\beta}\gamma/\beta$  is indeed an index of growth performance because it is in direct proportion to the mean anabolic rate. Similarly,  $\alpha^{-1/\beta}\gamma/K$  and  $\gamma/\beta$  in Equation 12 can be interpreted respectively as the average maximum size and growth rate of a species. The quotient  $(\gamma/\beta)/(\alpha^{-1/\beta}\gamma/K) = \alpha^{1/\beta}K/\beta$  is an index of catabolic performance, because it is in direct proportion to the mean catabolic rate.

Finally, anabolic and catabolic rates of animals can be estimated from data from a mark-recapture experiment on two distinct lengths of the same individual measured at different times. Thus, the present work has demonstrated a way to estimate anabolic and catabolic rates of animals. Such field-based estimates can be compared with those obtained under laboratory conditions.

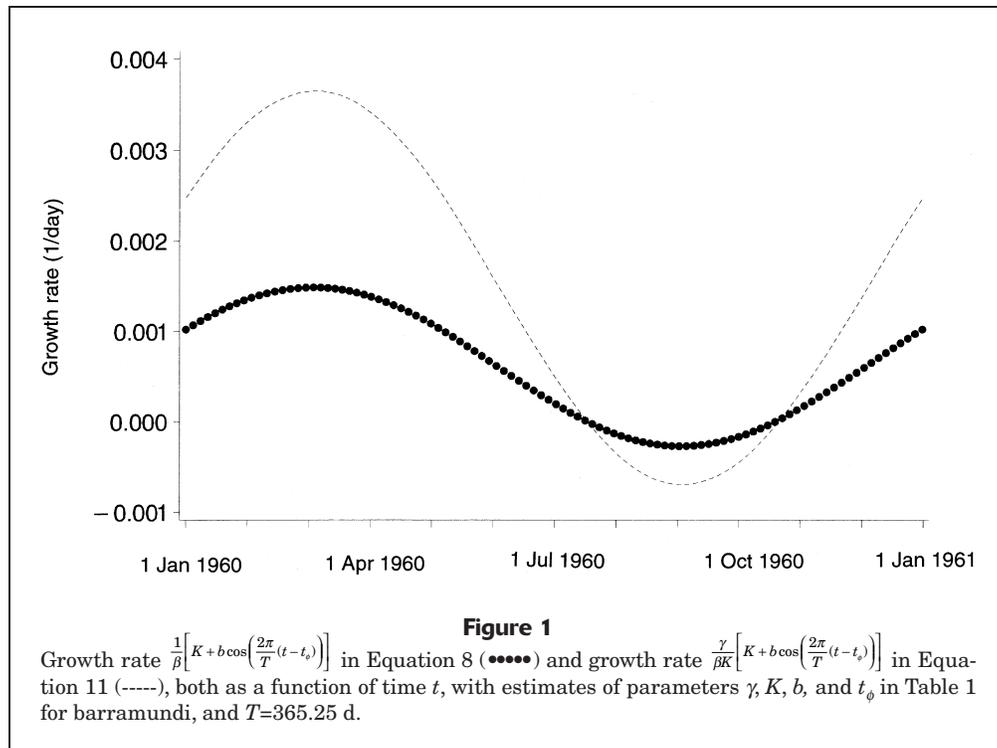
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**Table 1**

Estimates and (in parentheses) standard errors of parameters obtained by fitting Equations 6, 8, 9, 11, and 12 to barramundi tagging data using the least squares method under the assumptions that  $T = 365.25$  d, time started (i.e. time  $t=0$ ) in 1 January 1960, and errors in  $L(\alpha, t)$  follow independent normal distributions, with a mean of  $L(\alpha, t)$  and a constant variance of  $\hat{\sigma}^2$ .  $P < 0.0001$ ;  $n = 308$ .

Equation	$\hat{\gamma}$ (kg <sup>1-B</sup> /d)	$\hat{K}$ (kg <sup>1-D</sup> /d)	$\hat{b}$ (kg <sup>1-D</sup> /d)	$\hat{t}_0$ (d)	$\hat{B}$	$\hat{D}$	$df_p, df_D, F$	$\hat{\sigma}^2$	$r^2$
6	0.00843 (0.00008)	0.00556 (0.00005)	—	—	0.87213 (0.00148)	1.03567 (0.00216)	4,304,15424.6096	22.9793	0.9951
8	0.00474 (0.00052)	0.00184 (0.00034)	0.00265 (0.00054)	62.7197 (6.8279)	—	—	4,304,20333.2966	17.4525	0.9963
9	0.00500 (0.00062)	0.00196 (0.00040)	—	—	—	—	2,306,30966.0441	22.8923	0.9951
11	0.00446 (0.00036)	0.00206 (0.00023)	0.00302 (0.00045)	63.5155 (6.7581)	—	—	4,304,19947.9059	17.7884	0.9962
12	0.00487 (0.00044)	0.00228 (0.00028)	—	—	—	—	2,306,30895.5175	22.9443	0.9951



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